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NOTES ON THE *CHAMAELEO BITAENIATUS* COMPLEX

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NOTES ON THE *CHAMAELEO BITAENIATUS* COMPLEX

By A. S. Rand[1]

The lizards known as *Chamaeleo bitaeniatus* have long been considered a series of morphologically differentiated populations of a single widespread and quite variable species. This idea was first proposed by Tornier in 1896 and was accepted by Loveridge in his 1957 check list.

Examination of the collections in the Museum of Comparative Zoology and of the recent literature suggests that the situation is somewhat more complicated. Two of the forms considered as geographical races occurring in Kenya have been collected at the same locality without indication of intergradation. A similar situation is reported by Witte, 1941, and Laurent, 1952, for the mountains east of the African great lakes where two other "subspecies" occur together in the same area, though largely separated ecologically.

On the basis of the present study, six species are recognized: *C. rudis, C. bitaeniatus, C. ellioti, C. höhnelii, C. schubotzi,* and *C. kinetensis.* Three races of *C. rudis* are recognized: *C. r. rudis, C. r. schoutedeni* and *C. r. sternfeldi,* the latter described in this paper.

The *Chamaeleo bitaeniatus* complex is a group of medium-sized chameleons from the highland regions of East Africa, occurring both in the mountain forests and the highland savannas and ranging from the Abyssinian plateau in the north to the vicinity of Lake Nyasa in the south, and from the mountains west of the Rift in the Belgian Congo to the Chulu hills in Kenya. No members of the group are known from the mountains in easternmost Tanganyika, e.g., the Usambaras and the Ulugurus. The group is characterized by having the body scalation at least somewhat heterogeneous, by lacking (in both sexes) annulated horns, occipital lobes, tarsal spurs, axillary pockets and dorsal fins. All species possess a ventral, a gular, and a dorsal crest, formed in each case by a single row of enlarged scales, and they all show some indication of one or two rows of enlarged plates along the sides of the body. What evidence is available suggests that all give birth to live young.

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PREVIOUS WORK

Four revisions of this species complex have been attempted since Fischer first described *bitaeniatus* in 1884. No two of the revisers have come to the same conclusions, and I have yet a fifth arrangement to suggest.

Tornier, 1896, grouped the four species described to that date as races of *bitaeniatus*. He pointed out the closeness of relationships and concluded that each represented a segment of a morphological series. He used the dorsal and ventral crests, the body scalation, the shape of the casque, and the rostral projection as the characters on which to arrange the species. His series ran: *ellioti — bitaeniatus — leikipiensis — höhnelii*.

Sternfeld, in two papers in 1912, regarded the five described forms as races and named four additional ones. These nine forms he arranged in three morphological series, each descended from a stem form which he postulated as being close to *ellioti*. One line included *graueri, rudis* and *schubotzi*, the second *bitaeniatus, leikipiensis, höhnelii*, and *bergeri*, and the last only *tornieri*. In addition to the characters employed by Tornier, he used head and body proportions and the arrangement as well as the size of the various crests. He believed that intergrades connected all these forms.

Parker, 1932, apparently accepting as subspecies all the forms recognized by Sternfeld but omitting *C. bequaerti* Witte, 1922, divided the series into four groups. The first included *bitaeniatus, ellioti, graueri* and *tornieri*, the second, *rudis*, the third, *leikipiensis, höhnelii* and *bergeri*, and the fourth, *schubotzi*. He stated that the second group intergraded with the first through *graueri*, the third intergraded with the first through *leikipiensis-bitaeniatus*, and the fourth was distinct, combining some of the characters of group three with others of group two, but without intergradation. The characters cited are those used by Sternfeld.

Loveridge, 1957, in his East African check list, recognized six subspecies of *bitaeniatus: bitaeniatus, ellioti* (including as synonyms *graueri, tornieri* and *bequaerti*), *rudis* (including *burgeoni*), *schubotzi, höhnelii* (including *leikipiensis* and *bergeri*), and *altaeelgonis*. He also mentioned, in a footnote, *C. b. kinetensis* of Schmidt, 1943, as an intermediate between *bitaeniatus* and *ellioti*, and *C. b. schoutedeni* Laurent (1952) without comment. No discussion or documentation of these assignments was attempted in the check list.

Both Witte and Laurent have discussed sections of this group in relation to the forms in the mountains of the eastern Belgian Congo, and their conclusions are discussed under the appropriate forms.

These classifications differ primarily in the degree of splitting and in the places where the splits are made. The arrangement offered here differs basically from the others in that, on the ground of arguments from sympatry and character displacement, I have attempted to show that these divisions are of specific rather than subspecific value.

MATERIAL

This revision was based primarily on the large collection of chameleons in the Museum of Comparative Zoology (MCZ). Critical specimens were also borrowed from the American Museum of Natural History (AMNH), Chicago Natural History Museum (CNHM), California Academy of Sciences (CAS), British Museum (Natural History) (BMNH), and the Genoa, Berlin, Paris and Coryndon museums.

ACKNOWLEDGMENTS

I would like to thank the curators of the various museums cited above for their kindness in allowing me to examine specimens in their care. I would also like to thank Dr. E. E. Williams for his advice and assistance throughout.

CHARACTERS USED

The nine characters used in this paper are, with two exceptions, those used by Sternfeld. These two exceptions are the throat grooves in *ellioti* and the number of scales between junction of the canthal ridges and the upper labials, the latter a character used by Laurent, 1952, to define *C. rudis schoutedeni*. I have arranged the characters in the order of their apparent taxonomic usefulness.

1. *Parietal crest* (formed by the parietal bone). The shape of the parietal crest seen in profile varies considerably in these forms. In *höhnelii* it is high, rising steeply from the top of the head, and is strongly curved; in the other forms the crest rises considerably less steeply and is almost straight in outline. In dorsal view, the parietal crest is of nearly uniform width throughout its length, except in the *C. rudis sternfeldi* from

Kilimanjaro and Mt. Meru, where it widens posteriorly into a knob.

2. *Rostral projection.* In all specimens of *höhnelii* there is a scale-covered upward projection on the end of the snout (formed by the dorsal projections of the maxillary bones). There is considerable variation in the length of this projection and in the amount of lateral compression. This variation does not seem to be correlated with age, sex, or locality. A small rostral projection is present in some specimens of *C. rudis rudis,* but it differs from that of *höhnelii* in being very small, dorsoventrally compressed, and directed anteriorly.

3. *Ventral crests.* A row of enlarged scales is present along the ventral midline in all these forms. It may extend from the gular region to the vent as in most specimens; in *cllioti* it usually extends onto the base of the tail for a greater or lesser distance. This is also true for occasional specimens of *rudis* and *bitaeniatus* but not for *höhnelii.* In all forms the length of the scales forming the gular crest is greatest anteriorly and least posteriorly. This characteristic is strongly marked in *höhnelii,* which has a very long gular crest and a moderate pectoral crest. In the other forms, the gular crest is not as long and the difference between gular and pectoral crests is not nearly as marked. In *höhnelii* and some specimens of *C. rudis rudis* the longest scale in the gular crest measures between ⅓ and more than ½ the vertical diameter of the orbit; in all the other forms the longest scale is at most about ⅓ this distance. In *rudis* and *schubotzi* the ventral crest is very difficult to distinguish from the rest of the body scales on the posterior part of the belly. In many specimens of *C. r. schoutedeni* the gular crest is also very short. The crest is formed of scales that are either uniform in size or long and conical alternating with short ones. Usually the alternation of long and short scales occurs in animals with long crests and in those parts of the crest where the scales are longest.

4. *Body scalation.* The scales on the body, legs and tail of all these forms are somewhat heterogeneous. This characteristic is least marked in *cllioti,* well marked in *bitaeniatus, höhnelii* and *rudis,* and extremely well marked in *schubotzi.* In all the forms there is a tendency for one or two rows of large plates to be present along the side, the upper row running from the crest on the temporal arch back over the hind leg and sometimes continued on to the tail, and the lower row running from the axilla back to the hind leg. These may be absent in *cllioti,* or the upper one may be weakly developed. In *höhnelii, bitaeniatus* and *rudis*

the upper row is almost always present, although it may be interrupted and a lower row of plates slightly smaller in size may be present. In *schubotzi,* two rows of very large plates are present, the lower row as large or slightly larger than the upper; the diameter of the largest of these plates is greater than the length of the eye opening when the eye is closed. In all the other forms the plates are smaller or, rarely, equal.

5. *Throat grooves.* In the populations of *ellioti* from Kenya and eastern and northern Uganda, there are present on each side of the throat one or two long, sharply defined, longitudinal grooves, usually lined with black pigment. In the *ellioti* populations from farther south, these grooves are more numerous (up to four main ones), more branched, and not lined with black. This transition seems to be a gradual one, and the southern populations are scarcely distinguishable from the other species on the basis of this character.

6. *Shape of head. C. höhnelii, ellioti* and *bitaeniatus* have long, narrow heads, *rudis* and *schubotzi* short, broad heads. This difference can be expressed by comparing the greatest width of the head measured between temporal ridges with the length of the head measured from the tip of the snout to the end of the parietal crest. In *höhnelii* the head is more than twice as long as wide; in *ellioti* and *bitaeniatus* it is twice to slightly more than twice as long as wide; in *rudis* and *schubotzi* it is less than twice as long as wide (one specimen of *rudis* is just twice as long as wide). *C. ellioti* shows some geographical variation in this. The differences are even more striking in the palatal view of prepared skulls. The shape of the head is paralleled by the shape of the body, *höhnelii, ellioti* and *bitaeniatus* usually having laterally compressed, deep bodies, and *rudis* and *schubotzi* having squat, thick bodies. However, since body shape depends to such an extent on fixation, I have been unable to measure it convincingly.

7. *Pattern.* This is an extremely difficult character to use in distinguishing animals that are as variable as chameleons and on which I have so little information about color in life. All these remarks concern preserved specimens. Most specimens of *ellioti* (almost all those in which the body color is dark) have a ventral crest of a contrasting light color. My specimens of *bitaeniatus* are all light in color, as is their ventral crest. However, Fischer's (1884) description of *bitaeniatus* mentions a light, contrasting, ventral crest. Specimens of *rudis* and *höhnelii,* most of which are dark, have the ventral crest the same

color as the body. The two specimens of *schubotzi* are light, probably as a result of fading in alcohol.

Almost all my specimens of *ellioti* have a marked light-colored, lateral line; this is also indicated in the *bitaeniatus* and was mentioned by Fischer (1884). This line is lacking in *rudis* and *höhnelii*.

8. *Dorsal crest.* A dorsal crest, present in all forms, differs in the degree of development and in the relative size of the scales composing it. Usually, the crest is composed of units of three or four scales increasing in size posteriorly. The difference between the first and last scales in a series may be very great, as it is in *höhnelii*, or very slight, as it is in some specimens of *ellioti*. The other forms seem to be intermediate in this respect, and a great deal of individual variation is evident, particularly in *rudis*.

Key to the forms of the C. BITAENIATUS group.[1]

1. Parietal crest very high, strongly arched; a rostral projection present; gular crest long (longest scale ⅓ to more than ½ the vertical diameter of the orbit); belly crest short ..... *C. höhnelii*
   Parietal crest profile low to moderate, almost straight; no rostral projection; gular crest variable; belly crest short to moderate 2
2. Head less than twice as long as broad[2]; scalation heterogeneous; body squat in appearance 4
   Head about twice as long as broad or longer; scalation more or less heterogeneous; body laterally compressed 3
3. Scalation weakly heterogeneous; 1 or 2 well-marked throat grooves usually present; particularly in north of range (northern Uganda and the Sudan), these grooves frequently containing black pigment ..... *C. ellioti*
   Scalation much more strongly heterogeneous; 1 or 2 lateral rows of enlarged plates present; many shallow grooves on the throat ..... *C. bitaeniatus*
4. Scalation very strongly heterogeneous; 2 rows of very large plates (greatest diameter longer than aperture of closed eye) ..... *C. schubotzi*
   Scalation not so strongly heterogeneous; 1 or 2 rows of large plates (greatest diameter not longer than aperture of closed eye) 5
5. Parietal crest widening posteriorly, frequently forming a knob ..... *C. r. sternfeldi*
   Parietal crest not widening posteriorly 6
6. Junction of canthal ridges separated from labials by 1 or 2 scales; gular crest very short ..... *C. r. schoutedeni*

[1] Omitting *C. kinetensis*.
[2] In very young individuals the head is proportionately broader.

Junction of canthal ridges separated from labials by 3 or 4 scales; gular crest moderate to long ..... *C. r. rudis*

Chamaeleo höhnelii Steindachner

1891 *Chamaeleon höhnelii* Steindachner, Sitzb. Akad. Wiss. Wien, 100, Abt. 1: 309, pl. 1, figs. 1-1a. Laikipia, 6000 ft., Kenya Colony.

1891 *Chamaeleon leikipiensis* Steindachner, Sitzb. Akad. Wiss. Wien, 100, Abt. 1: 311, pl. 1, figs. 2-2a. Laikipia, 6000 ft., Kenya Colony.

1912 *Chamaeleon bitaeniatus bergeri* Sternfeld, Wiss. Ergeb. deutsch. Z. Afr. Exp., 4: 252. Sergoit, north of Eldama Ravine Station, Kenya Colony (erroneously given as "Sirgoi, südlich von Ravine" in the original description).

1935 *Chamaeleon bitaeniatus altaeelgonis* Loveridge, Bull. Mus. Comp. Zool., 79: 15. Kaburomi, 10,500 ft., Mount Elgon, Uganda.

1957 *Chamaeleo bitaeniatus höhnelii:* Loveridge, Bull. Mus. Comp. Zool., 117(2): 201.

1957 *Chamaeleo bitaeniatus altaeelgonis:* Loveridge, Bull. Mus. Comp. Zool., 117(2): 201-2.

Description. The parietal crest, in profile, rises steeply and then curves sharply downwards, so that the highest point is anterior of the posterior end of the crest. The profiles vary from a condition with a very steep anterior border and a sharp curvature (so that the profile is almost square) to one in which the rise and fall is much more gentle. The crest is always higher and more strongly curved than in any other species. It is uniform in width.

The crests alongside the parietal crest rise from the posterior end of the supraorbital crest and curve medially and posteriorly to run parallel to the parietal crest for a short distance. They may, but usually do not, join this crest. They are usually distinct but may be weak.

A short rostral projection, usually somewhat laterally flattened, is always present. It projects dorsally from the tip of the snout and is scale covered. There is considerable variation in size and lateral flattening in this projection, apparently uncorrelated with sex or age. A rostral projection occurs in both hatchlings and well developed embryos.

The dorsal crest is strongly developed. It is made up of groups of three to five scales. Within each group the scales increase in size posteriorly, with the last two much larger than those preceding them and the very last two or more times larger than the one in front of it.

The gular crest is long, the longest scales a half to more than a half the vertical diameter of the orbit. The crest on the belly is much shorter, and in some cases the scales composing it are only slightly larger than the surrounding belly scales; it is not continued on the tail. The long conical gular-crest scales usually alternate with small scales that may be either single or paired.

The scalation is strongly heterogeneous on the body, the upper surfaces of the legs and the tail, the large scales being strongly convex. The largest scales, separated by small scales, are arranged in a row running from the neck back of the temporal arch to above the hind legs, sometimes continuing a short distance on the tail. A second series of enlarged scales, which are separated by small scales and which are smaller than those in the upper row but larger than the enlarged scales between the two rows, is usually present below the upper row.

There are many small, shallow grooves on the throat. The head is considerably longer than broad. The body usually appears somewhat laterally compressed. In alcohol the specimens appear uniformly dark.

Discussion. The relationships of this form to the others recognized here are discussed later (pp. 22-27).

Four names have been applied to this species. Three of these appear to be based on individual variation. Sternfeld, 1912b, proposed *bergeri* for those specimens in which the nasal projection, the high casque, and the gular crest were most exaggerated; he used *leikipiensis* Steindachner, 1891, for those in which these characters were least well developed, and restricted *höhnelii* to those that were intermediate in these characters. The examination of several large series in the Museum of Comparative Zoology shows no correlation of variation in these characters with sex, size, or geography. *Bergeri* and *leikipiensis* are therefore considered direct synonyms of *höhnelii*.

The fourth name, *altaeelgonis*, was proposed for a population occurring at high altitudes on Mt. Elgon and differing from the population at lower altitudes on this same mountain only in size. Until we know more about the phenotypic effects of altitude on the growth of these reptiles, and about the populations living at high altitudes on other mountains, it seems best to consider this also a synonym of *höhnelii*.

Material examined. **Kenya.** Njoro, Rift Valley Prov., *ca.* 7,500 ft.: MCZ 61179, CNHM 58267-76, 79068-90. Molo, Mau Plateau, 9,000 ft.: MCZ 34994, CNHM 2295, 6425-29. Mt. Kenya: MCZ 29457-58, CNHM 2299, 2304. Nani Moru Track,

Mt. Kenya, 10,000 ft.: MCZ 57198. Kenia Forest (= Mt. Kenya?): MCZ 11489. Hills west of Mt. Kenya: MCZ 7839. Voi: CNHM 2307-08. Lagari: CNHM 1845. Kijaba: CNHM 2281. Lukenya: CNHM 2288-89. Lukenya Hills, Athi Plains: CNHM 2292-93. Four mi. W. of Nyeri, 1,660 m.: CAS 86010. Wambugu: MCZ 29469-88(50). Nakuru: MCZ 13360. Loita Plains, Mau Escarpment, S. Masai Reserve, 7,000 ft.: MCZ 17992. Lengetia, Mau Narok, 9,000 ft.: MCZ 62230. Fort Hall: MCZ 29459-68. S. Kinangop Plateau, 10,000 ft.: MCZ 47251-52. Elgonyi, S. Mt. Elgon, 7,000 ft.: MCZ 41800. Kabete, nr. Nairobi: MCZ 31384-85.

Uganda. Budadiri, Mt. Elgon, 4,000 ft.: MCZ 41796-99. Butandiga, west Mt. Elgon, 6,000 ft.: MCZ 41771-95(25). Sipi, west Mt. Elgon, 6,500 ft.: MCZ 41751-69(52). Kuburomi, west Mt. Elgon, 10,500 ft.: MCZ 40274-300. Bulambuli, west Mt. Elgon: MCZ 41770. Madangi, west Mt. Elgon, 11,000 ft.: MCZ 41801-02.

Chamaeleo bitaeniatus Fischer

1884 *Chamaeleo bitaeniatus* Fischer, Jahrb. Hamburg. Wiss. Anst., 1: 23, pl. ii, figs. 7a-b. Lake Naivasha, Kenya Colony.

1887 *Chamaeleo bivittatus* (lapsus: *nomen nudum*) F. Müller, Verh. Naturf. Ges. Basel, 8: 294. Witu, Kenya Colony.

1957 *Chamaeleo bitaeniatus bitaeniatus:* Loveridge, Bull. Mus. Comp. Zool., 117: 200.

Description. The parietal crest in profile is low and straight, or nearly so, rising gradually, posteriorly, so that the highest point is at or near the posterior end. The crest is frequently slightly curved so that in profile the posterior part is parallel to the mouth opening. The parietal crest is approximately uniform in width.

The crests on each side of the parietal crest are nearly straight and run from between the orbits back to parallel the parietal crest on each side for almost half its length. Anteriorly they usually extend laterally to meet the supraorbital crest, frequently above the eye and occasionally behind the orbit. Posteriorly they usually do not join the parietal crest, but are separated from it. These crests are usually distinct, but occasionally they may be obscured by other projections in this area.

There are no rostral projections.

The dorsal crest is moderate in size and composed of groups of 2-5 scales, increasing strongly posteriorly within each group.

Usually the first and second scales of each group do not have the conical, laterally compressed shape of the larger, more posterior ones. Ordinarily the last scale in each group is markedly larger than the one just before it.

Ventral and gular crests are moderately developed, the gular crest being longer but not strikingly so. The largest scales in the gular crest are frequently anteroposteriorly flattened and rarely separated by small scales. Occasionally a continuation of the ventral crest onto the tail is indicated.

The body scalation is markedly heterogeneous, always with an upper row of large plates (which are the largest scales on the body) and almost always with a lower row of large plates. The plates in the upper row are very numerous and frequently in contact. They are never strongly convex.

There are numerous shallow grooves on the side of the throat. The head is narrow, more than twice as long as wide.

The preserved specimens are usually light in color, with indications of light lateral lines following the rows of enlarged plates. The ventral crest is light in color but not markedly lighter than the body, although Fischer (1884) comments that the type had a light ventral line. Preserved specimens usually appear laterally compressed.

Discussion. The relationships of this form to the others recognized here are discussed later (pp. 22-27).

C. bitaeniatus Fischer, 1884, was the first name applied to any of these chameleons. Since that time, only one other name has been used for this species, *C. bivittatus* Müller, 1887. This name appears in a catalogue of the herpetological collections of the Basel Museum, with only a collector and a locality following it. A *nomen nudum*, it is apparently a lapsus for *bitaeniatus*.

Since Tornier (1896), *C. bitaeniatus*, as a binomial, has been used frequently to apply to chameleons in this group. As discussed under *ellioti*, Loveridge in 1942 and in the 1957 check list included specimens of *C. ellioti* under *C. b. bitaeniatus*. As discussed under *C. rudis*, Hellmich, 1956, referred to specimens of that species from southern Tanganyika as *C. b. bitaeniatus*.

C. kinetensis Schmidt, 1943, which may belong here, is discussed below.

Material examined. **Kenya.** Subukia, Nakuru Dist., Rift Valley Prov., 7,000 ft.: CNHM 58266, 79105. Lukenya Hills, Athi Plains: CNHM 2287, 2290, 2291, 2294(2). Lukenya: CNHM 2282-83, 2297. Kijabe: CNHM 2285-86. Kedong Valley: CAS 66018. Athi River, 1,500 m.: CAS 85751. Bukori, S. foot of Mt.

Elgon: MCZ 41715-21. Loita Plains, Mau Escarpment, S. Masai Reserve, 7,000 ft.: MCZ 17995-97. Plains N. of Mt. Kenya: MCZ 8184. Hills W. of Mt. Kenya: MCZ 58228. Plains by Guaso Nyiro: MCZ 7838. Mtito Andei: MCZ 29906. Near Meru River: MCZ 7837. Laikipia: MCZ 8183. Lake Naivasha, Coryndon, Chulu Hills: MCZ 29453.

Tanganyika. Longido West: MCZ 13561.

Ethiopia. Addis Ababa: Genova CE 27995. Between Saneurar and Amarr (Boran): Genova CE 28815. Between Badditu and Oime: Genova CE 28816.

Somalia? Coronna: Genova CE 2888(2).

Chamaeleo ellioti Günther

1895 *Chamaeleon ellioti* Günther, Ann. Mag. Nat. Hist., (6) 15: 524, pl. xxi, fig. A. Kavirondo, 3900-4000 ft. and foot of Mt. Ruwenzori 5-6000 ft. Restricted by Loveridge to Bugoye, east foot of Ruwenzori Mountains, Uganda.

1922 *Chamaeleon bequaerti* Witte, Revue Zool. Bot. Afr., 10: 69, pl. ii, fig. 1. Beni, Kivu Dist., Belgian Congo.

1942 *Chamaeleo bitaeniatus ellioti:* Loveridge, Bull. Mus. Comp. Zool., 91: 365.

1942 *Chamaeleo bitaeniatus bitaeniatus:* Loveridge, Bull. Mus. Comp. Zool., 91: 364-5.

1957 *Chamaeleo bitaeniatus ellioti* (part): Loveridge, Bull. Mus. Comp. Zool., 117: 200.

1957 *Chamaeleo bitaeniatus bitaeniatus* (part): Loveridge, Bull. Mus. Comp. Zool., 117: 200.

Description. The parietal crest is like that of *C. bitaeniatus.* The crests lateral to the parietal crest are like those in *bitaeniatus,* exeept that they usually join the supraorbital crest over the eye anteriorly, and posteriorly they usually curve medially to meet the parietal crest.

There is no rostral projection.

The dorsal crest is quite low. It is formed of groups of 2-5 scales that increase in size posteriorly, though without the great differentiation typical of other species, particularly *höhnelii.*

The gular erest is low and quite uniform; the largest scales are usually laterally compressed triangles, not alternating with small scales. The ventral crest is distinct, slightly lower than the gular crest, and usually continued a short distanee on the tail.

The body scalation is much more homogeneous than in *bitaeniatus.* An upper row of enlarged scales is frequently present,

but the scales are really quite small, never much larger than surrounding large scales and not in contact; a lower row of somewhat enlarged scales is sometimes present.

Particularly in the northern populations, one or two deep, black-lined grooves are present on the side of the throat.

The head is at least twice as long as broad. There is some geographical variation in this character, the specimens from southwest Uganda and the Congo having narrower heads than do those from Kenya.

In alcohol this species is usually dark, with a clear light lateral line and with the ventral crest lighter than the belly.

Preserved specimens are usually laterally compressed.

Discussion. The relationships of this form to the others recognized here are discussed later (pp. 22-27).

The oldest name for this species is *ellioti,* and Günther's description and figure clearly show the black-lined grooves along the throat, characteristic of the northeastern populations of this species.

C. bequaerti is well described by Witte, 1922, from Beni, Congo, and his figure shows clearly black-lined throat grooves. In his concluding paragraph, Witte writes that Boulenger examined the type and considered it intermediate between *C. senegalensis* and *C. ellioti* and very close to the latter. Witte does not discuss the differences which led him to separate *bequaerti* from *ellioti,* and there is nothing in the description nor in a single paratype from Beni (now in the Museum of Comparative Zoology) that serves to distinguish them. It seems advisable to consider them synonymous.

Loveridge, 1942, on the basis of specimens collected in Uganda, recognized *ellioti* as distinct from *bitaeniatus.* He writes, ". . . one can separate *ellioti* by its longer gular-ventral and dorsal crests, the latter being brick red or dried-blood red (orange in typical *bitaeniatus*)." These are colors in life. My examination of these specimens from Uganda assigned by Loveridge to *bitaeniatus* show them to agree with *ellioti* in scalation and in possession of throat grooves, and to differ in these characters from typical *bitaeniatus* from Kenya. They are therefore referred by me to *ellioti.* The differences in color noted by Loveridge are not visible on preserved specimens, and while such color differences represent significant intraspecific variation in *ellioti,* they do not reflect the specific difference between *ellioti* and *bitaeniatus.*

Material examined. **Kenya.** Kitale, 6,000 ft.: MCZ 53968. Kericho: MCZ 52196-97. Yala River: MCZ 18361-62. Kaimosi, Kakamega: MCZ 41722-50.

Uganda. Behungi Escarpment, Kigezi Dist.: CNHM 9866-69. Kisolo, Lake Mutanda, Virunga volcanoes, 6,000 ft., Kigezi Dist.: CNHM 9870-71, 9873, 9875-76, 9878, 9880-82. Mushongero, Lake Mutanda, 5,924 ft.: MCZ 47214-15. Kibale Forest, Toro: MCZ 47191-99. Mabira Forest, nr. Jinja: MCZ 31184-85. Mubango, Mabira Forest: MCZ 47178-90. Entebbe: MCZ 31161-83. Nyakabande, Kigezi Dist., 6,925 ft.: MCZ 47212-13. Mihunga, Ruwenzori Mts., 6,000 ft.: MCZ 47210-11. Bugoye, Ruwenzori Mts.: MCZ 47201-09. Mt. Ruwenzori, 6,000 ft.: CNHM 1844(2). Lukungu Mts., W. Mt. Elgon: MCZ 41621-22. Kampala: MCZ 7258(3). Bundibugyo, Bwamba Region: MCZ 47200. Fort Portal: AMNH 49915.

Rwanda. Kisenyi, N. shore of Lake Kivu, 1,460 m.: CNHM 12782, MCZ 24838-42(8). Kiranga, nr. Kisenyi: MCZ 47216-50(67). Lake Kivu: MCZ 37143.

Congo. Beni, Semliki Valley: MCZ 43029, CNHM 12762. Mambawanga Hill, 40 mi. W. of Beni: CNHM 12806. Rutshuru, Kivu Dist.: MCZ 24829-32, CNHM 12832. Ruwenzori Mts., 3,000 m.: CAS 85987. Tshibati (Lwiro), 32 mi. N. of Bukavu, 1,950 m.: CAS 85763-67. Lulenga, N. of Lake Kivu, 6,000 ft.: MCZ 24843-60.

Tanganyika. Kabare, Bukoba: MCZ 18722-23. Rungwe [loc. questioned]: AMNH 47361-71.

Sudan. Kipia, Imatong Mts. 8,700 ft.; MCZ 45267.

Chamaeleo rudis rudis Boulenger

1906 *Chamaeleon rudis* Boulenger, Ann. Mag. Nat. Hist., (7) 18: 473. Ruwenzori Mountains above 10,000 ft., Uganda.

1912 *Chamaeleon bitaeniatus graueri* Sternfeld, Wiss. Ergeb. deutsch. Z. Afr. Exp., 4: 250. Rugege and Bugoie Forests, Ninagongo, 2500-3000 m. and Ruwenzori, *ca.* 25000 m.

1912 *Chamaeleon bitaeniatus tornieri* Sternfeld, Sitzb. Ges. Naturf. Freunde, Berlin, 1912: 383, pl. xvii, fig. 35. Lendu Plateau, Ituri Dist., Belgian Congo.

1933 *Chamaeleon burgeoni* Witte, Revue Zool. Bot. Afr., 24: 120. Mombasa, near Lubero, Kivu Dist., Belgian Congo.

1957 *Chamaeleon bitaeniatus rudis:* Loveridge, Bull. Mus. Comp. Zool., 117: 201.

1957 *Chamaeleon bitaeniatus ellioti* (part): Loveridge, Bull. Mus. Comp. Zool., 117: 200.

Description. The parietal crest profile is like that of *bitaeniatus,* except that in one specimen from Kenya assigned to *C. rudis* the crest is very high, although straight.

The crests lateral to the parietal crest are like those in *höhnelii,* except that they sometimes do not meet the supraorbital crests. There are three to four scales between junction of canthal ridges and the supralabials.

In most specimens there is no rostral projection. In some specimens of *C. rudis rudis* from the Lake Kivu area, the junction of the canthal ridges projects slightly forward to form a small dorsoventrally flattened projection.

The gular crest varies from very long in some specimens of *C. rudis rudis* from the Ruwenzori Mountains to moderately short in others. The large scales are conical, frequently alternating with small ones. The ventral crest is shorter than the gular crest, frequently almost indistinguishable, and very occasionally continued a short distance on the tail.

The body scalation is usually moderately heterogeneous, with an upper row of enlarged scales usually present and the lower row sometimes present. The enlarged scales, not much greater than other large scales, are strongly convex.

There are many small, shallow, throat grooves. The head is broad, less than twice as long as wide. The preserved specimens show little or no lateral flattening of the body. In alcohol the specimens are usually uniformly dark.

The dorsal crest is variably enlarged and made up of groups of scales composed of 1 to 3 small scales, one medium-sized laterally compressed scale and, finally, one large laterally compressed scale.

Discussion. Four names have been proposed for the broad-headed chameleons living in the Ruwenzori Mountains and the mountains south to Lake Kivu. The oldest of these is *C. rudis* Boulenger, 1906, who distinguished it from *bitaeniatus* on its "coarser scaling and in the much larger scales forming the gular and ventral crest, the longest of these on the throat, measuring half the diameter of the orbit." Sternfeld, 1912, described *graueri,* distinguishing it from *rudis* on the basis of its having the gular crest scales less enlarged. He apparently did not realize that this name was preoccupied by *C. graueri* Steindachner, 1911, a synonym of *C. johnstoni.*

Mr. Battersby has kindly made a detailed comparison of the type of *rudis* with a cotype of *graueri.* He reports (letter of April 24, 1959) that the longest scales are "a little smaller than

size of the eye opening or about ½ to ¼ the orbital ring'' in the type of *rudis* and ''about ⅔ of eye opening or ⅕ of orbital ring'' in the cotype of *graueri*. He also lists several other scale characters in which these two differ. He also says that though these characters are difficult to define, he feels a ''sense'' of difference. Though the subjective impression of an experienced systematist is often more reliable than many objective measurements, I feel that, since all the characters he mentions show considerable individual variation in other populations, *graueri* should be considered for the present conspecific with *rudis*.

Loveridge, 1957, regarded *graueri* as a synonym of *ellioti*. *C. graueri,* with its heterogeneous scales and broad head, even if not identical with *rudis,* as here believed, is certainly much closer to it than to *ellioti*.

Sternfeld, 1912b, described *C. tornieri* as like *ellioti* in habitus but differing from it in having a short, broad head. Since I have been unable to examine the type, my assignment of this form is based on his description and figures and is only tentative. It is included here because of his emphasis on its short, broad head. However, he quotes field color notes as ''Kehlfalten grünblau oder blau.'' It is possible that this refers to grooves on the throat that occur in *C. ellioti* but not in *C. rudis;* however, these, if present, are not evident in the photograph published with the original description.

Witte, 1933, described *C. burgeoni* from the mountains north of Lake Kivu as close to *rudis* and differing from it only in the presence of small lateral protuberances on the end of the snout. In 1941, he considered it conspecific with *bitaeniatus* and himself questioned its distinctness from what he called *C. b. graueri* (= *rudis*). His hesitancy in giving it subspecific status is understandable since at every locality where he collected *burgeoni* he also took *rudis*. Laurent, 1952, when he described *schoutedeni* from further south, apparently re-examined Witte's material and decided that *burgeoni* was indistinguishable from the other broad-headed chameleons (*graueri* = *rudis*) occurring with it. He pointed out the closeness of relationship between *rudis* in the Ruwenzori, the population near Lake Kivu (for which the name *burgeoni* is available since *graueri* Sternfeld 1912 is preoccupied by *C. graueri* of Steindachner, 1911), and his new *schoutedeni*. He was somewhat dubious about the validity of *burgeoni*.

I can find no consistent differences between the MCZ specimens from the Ruwenzori Mts. and those from near Lake Kivu,

and I consider *C. burgeoni* a synonym of *C. rudis rudis*. However, there are specimens from the Kivu area which do have a small nasal protuberance not seen elsewhere and some specimens from the Ruwenzori Mountains have gular crests longer than any that occur outside that area.

Material examined. **Uganda.** Kisolo, Lake Mutanda, Virunga volcanoes, Kigezi Dist.: CNHM 9872, 9874, 9877, 9879. W. slope Mt. Ruwenzori, 12,400 ft.: AMNH 47433.

Rwanda. N. slope of Mt. Karisimbi, 11,000 ft.: AMNH 47442. Lukumi, Mt. Karisimbi, 12,000 ft.: AMNH 47445.

Congo. Ruwenzori Mts., west slope of Stanley Group, 3,300 m.: CAS 85720-22. Tembwe: MCZ 42895. Kabara, Kivu volcanoes, 11,000 ft.: MCZ 42348-49. Kabara, S.W. Mikeno, 10,600 ft.: MCZ 24827. Ruero, S.W. slope of Mt. Mikeno, 9,000 ft.: AMNH 47444. Mt. Ninagongo (= Mt. Niragongo), 9,200 ft.: MCZ 29826. Karambi, E. of Rutshuru, 6,000 ft.: MCZ 24828.

Chamaeleo rudis schoutedeni Laurent

1952 *Chamaeleo bitaeniatus schoutedeni* Laurent, Rev. Zool. Bot. Afr., 46: Kabumbe Valley, 2400 meters, Kabobo Mountain, Albertville Terr., Tanganyika Prov., Belgian Congo.

Description. Like *C. rudis rudis* but differing from it in having 1 to 2 scales between the junction of the canthal ridges and the supralabials rather than 3 to 4, and in having, in most specimens, very short gular and ventral crests.

Discussion. Laurent, 1952, proposed the name *C. bitaeniatus schoutedeni* for the broad-headed chameleons that he found on Kabobo Mountain. He pointed out their close relationship to the broad-headed forms farther north and distinguished his new form on the basis that it possessed one or two scales between the junction of the canthal ridges and the supralabials rather than the three or four in the typical subspecies, and that the majority of the specimens of *schoutedeni* had a very much reduced gular, and ventral crests. The only two specimens I have seen from Mt. Kabobo certainly conform to Laurent's description and are different from the *C. rudis* from farther north.

Material examined. **Congo.** MCZ 59160-61: River Kabumbe, 2350-2400 m., Mt. Kabobo, Albertville Terr.

Chamaeleo rudis sternfeldi subsp. nov.

Type: MCZ 56173 ♂, Laikinae, Mt. Meru; Arusha dist.; Northern Prov., Tanganyika Terr., 7,500 ft. alt., August, 1957. Collected by C. J. P. Ionides.

Paratypes: MCZ 56165-72, 56174-75, 2 ♂ 7 ♀, 1 skeleton: same data as type. MCZ 44526: Mt. Meru east at 9,000 ft., B. Cooper, 1938. Berlin 17550 (one of the cotypes of *schubotzi*): Kilimanjaro. Paris 23*103: Kilimanjaro.

Diagnosis. A chameleon of the *C. rudis* group, differing from all the known forms in having the parietal crest always swollen posteriorly and forming in some individuals a distinct knob. Body scalation moderately heterogeneous; 3 to 4 scales between the junction of the canthal ridges and the labials; gular and ventral crests short.

Description. Body stocky; head short and broad, i.e., distance from tip of snout to end of parietal crest less than twice greatest width measured between temporal ridges in type and twelve paratypes (slightly greater in one paratype with extremely developed parietal crest); parietal crest swollen posteriorly (strongly in type and eight paratypes, weakly in four paratypes and not swollen in one paratype). Parietal crest in profile moderate and almost straight. No rostral projection. Ventral crests weak and composed of subequal scales, longest on the throat (longest ¼ vertical diameter of eye or less) where they are cone shaped and occasionally the most anterior ones alternate with small scales; posteriorly the scales are shorter and anteroposteriorly flattened, very indistinct on posterior belly; crest not continued on to tail.

Dorsal crest weakly developed in type and most paratypes (slightly stronger in three paratypes), composed of scales in groups of three anteriorly and four posteriorly, increasing posteriorly in size within the group though only moderately.

Scalation heterogeneous; sides of body and tail and upper surfaces of limbs covered with irregularly-sized, convex, small scales interspersed with larger convex scales. In the type the largest of these form a row running from the neck just behind the temporal crests to the base of the tail; a second row of scales slightly smaller than these runs from just behind and above the shoulder to just in front of the hind leg. The row is much less distinct and more irregular. The upper row is at least indicated in all specimens; the lower row is present in five paratypes and absent in five; in no specimen is the largest scale as large as the length of the closed eye opening. The sides of the throat show no indication of well marked grooves. No definite pattern is discernible in any of these specimens.

Chamaeleo rudis sternfeldi subsp. n.

Measurements of type and paratypes in mm.

Specimen	*Sex*	*Snout-vent length*	*Head length*	*Head width*
Laikinoi, Mt. Meru				
MCZ 56165	Female with eggs	84	23	13
MCZ 56166	Female with eggs	80	23	13
MCZ 56167	Skeleton			
MCZ 56168	Male	75	23	13
MCZ 56169	Female with eggs	68	20	11
MCZ 56170	Female with eggs	77	21	11
MCZ 56171	Female with eggs	82	23	11
MCZ 56173, *Type*	Male	81	24	14
MCZ 56174	Female with eggs	73	21	11
MCZ 56175	Male	62	21	12
Mt. Meru east				
MCZ 44526	?	72	20	11
Mt. Kilimanjaro				
Berlin 17750	?	48	17	9
Paris 23 * 103	?	79	22	12

Chamaeleo rudis subspecies

There are seven specimens of *C. rudis* which do not fit the classification given above. Three of these are from Embagai, Tanganyika. Like *C. rudis schoutedeni,* they have a very weakly developed gular crest, but the canthals are more widely separated from the labials than in typical *schoutedeni.*

A specimen is known from the Loita Plains on the Mau Escarpment in Kenya. At this same locality, both *C. bitaeniatus* and *C. höhnelii* were collected. This specimen differs from others in that the parietal crest rises more steeply posteriorly.

A single specimen from Gilo in the southern Sudan is most like *C. r. rudis,* but geographically widely separated. More material is necessary to determine its true relationships.

Two specimens from Litembo east of Lake Nyasa, which Hellmich, 1956, described under the name *C. b. bitaeniatus,* have not been examined but from his description seem to be *C. rudis.*

Material examined. **Sudan.** Gilo, 6,000 ft.: CNHM 47600.

Kenya. Loita Plains, Mau Escarpment, S. Masai Reservation, 7,000 ft.: MCZ 17994.

Tanganyika. Embagai, above Ngaruka: BM(NH) 1938.1.16. 18-20.

Chamaeleo kinetensis Schmidt

1943 *Chamaeleo bitaeniatus kinetensis* Schmidt, Field Mus. Nat. Hist., Zool., Ser., 24: 336. Mount Kineti, Imatong Mountains, Anglo-Egyptian Sudan. Altitude 10,458 ft.

Discussion. Schmidt, 1943, proposed the name *C. bitaeniatus kinetensis* for a single specimen from Mt. Kineti in the Sudan, which he felt was "allied to *Chamaeleo bitaeniatus ellioti* from which it is distinguished primarily by its smaller size and less uniform dorsal crest." I have examined this specimen and find that it lacks the throat grooves found in the single specimen of *ellioti* I have seen from this area. In most respects it resembles *bitaeniatus*, but the body scalation is more homogeneous than in any other *bitaeniatus* and no more heterogeneous than many *ellioti*. I cannot with confidence assign it to any of the species recognized here, nor am I convinced that it represents an additional full species. I suspect that it is an aberrant *C. bitaeniatus*, but whether an aberrant individual or a representative of an aberrant population I cannot tell. Until further material is available, it seems best to suspend judgment and provisionally recognize *C. kinetensis* as a full species.

Material examined. **Sudan.** Mt. Kineti, Imatong Mts.: CNHM 34483, Type.

Chamaeleo schubotzi Sternfeld

1912 *Chamaeleon bitaeniatus schubotzi* Sternfeld, Wiss. Ergeb. deutsch. Z. Afr. Exp., 4: 252. Mt. Kenya, 1400 ft., Kenya Colony (restricted by Parker, 1932).

1932 *Chamaeleon bitaeniatus schubotzi:* Parker, Journ. Linn. Soc. London, Zool., 38: 227.

1957 *Chamaeleo bitaeniatus schubotzi:* Loveridge, Bull. Mus. Comp. Zool., 117: 201.

Description. The parietal crest is like that of *bitaeniatus* in profile. It is not swollen posteriorly.

The crests lateral to the parietal crest arise from the supraorbital crests behind the orbits and curve posteromedially to meet the parietal crest, much as in *höhnelii*.

There is no rostral projection.

The gular crest is moderately low; the long scales are sometimes separated by small, paired scales. The ventral crest is slightly shorter than the gular crest and not continued on the tail.

The body scalation is very heterogeneous, more so than in any

other species. There are two lateral rows of enlarged plates, the largest greater than the length of the closed eye.

The dorsal crest is made up of groups of scales, usually two to four small granules followed by two or three enlarged scales that increase in size posteriorly.

There are many shallow throat grooves. The head is broad, less than twice as long as broad. The preserved specimens show no lateral flattening of the body. In alcohol, the specimens show no lateral or ventral stripes.

Discussion. C. schubotzi was described by Sternfeld on the basis of three specimens, with dubious localities. Parker (1932) later assigned a specimen from Mt. Kenya to this species and restricted the type locality to Mt. Kenya. I have examined two of Sternfeld's specimens, an adult labeled Mt. Kenya and a juvenile labeled Mt. Kilimanjaro, as well as Parker's specimen. The Berlin specimen labeled no. 15409, from Kenya, collected by Kolb, and Parker's specimen agree with Sternfeld's description of *schubotzi*. The juvenile, however, does not. It does match other specimens from Mt. Kilimanjaro described here as *C. rudis sternfeldi*. (For this reason it seems advisable to select the larger Berlin specimen no. 15409, from Mt. Kenya, as the lectotype of *C. schubotzi* Sternfeld.) These broad-headed specimens with extremely heterogeneous scales seem related to *rudis* and to be geographical representatives of it. However, the morphological difference between *schubotzi* and *rudis* is greater than that between any two populations of *rudis*. For this reason it seems best to recognize *schubotzi* as a full species.

Material examined. **Kenya.** Mt. Kenya: Berlin 15409, Type. Mt. Kenya, 14,000 ft.: BM(NH) 1932.5.2.110.

DISCUSSION OF RELATIONSHIPS

Two forms have been collected commonly in the highlands of Kenya. One, *höhnelii*, is an animal of the higher mountains. It has a nasal projection, a very high casque and a very long gular crest. In each of these characteristics it shows much individual variation that does not seem correlated with sex, age, or with geographical distribution. A population occurs at very high altitudes on Mt. Elgon which differs in smaller size from the typical *höhnelii* lower down on the mountain.

Occurring on many of these same mountains, but apparently at lower altitudes and not so closely associated with the mountain forest, is a form, *bitaeniatus*, lacking the specializations of

höhnelii and having very heterogeneous scalation, in which the large scales are flat or very weakly convex. *Bitaeniatus* and *höhnelii* occur in the same general area, and though they are apparently separated altitudinally, there are several collections containing both from the same localities (Loita Plains, Mau Escarpment; Lukenya; Lukenya Hills; Kijabe; hills west of Mt. Kenya). Since they seem to be, at least to some extent, sympatric, and since I have been unable to find any indications of intergradation even in the locality from which we have both forms, I feel *höhnelii* can no longer be considered a subspecies of *bitaeniatus* but must be called *Chamaeleo höhnelii*. *C. bitaeniatus* also occurs on Longido West in northern Tanganyika and in the mountains of Ethiopia and Somali Republic.

As one proceeds west in Kenya toward Lake Victoria, *bitaeniatus* is abruptly replaced by another form, *ellioti*, also with a head about twice as long as broad, with one or two distinct grooves (usually lined with black) on the sides of the throat, and with much less heterogeneous scalation. These two, *ellioti* and *bitaeniatus*, seem to have the same habitat preferences and to replace each other geographically; there is as yet no evidence of sympatry, though their ranges interdigitate to some extent. These have been considered subspecies, and I would continue this assignment except for the pattern of geographical variation in *ellioti*. *Ellioti* and *bitaeniatus* are very similar in body shape and in ornamentation and apparently in color in life, except for the differences in degree of heterogeneity of scalation and the striking black throat grooves in *ellioti*. These throat grooves are very distinct and usually black in the populations of *ellioti* from east of Lake Victoria and in those from northern Uganda across to the Ruwenzori Mountains and in one specimen from the Imatong Mountains. However, as one goes south in Uganda on the west side of the lake, the grooves become more numerous and less distinct (due to branching), and much less frequently lined with black, until in the mountains around Lake Kivu and those west of Lake Tanganyika, they are quite indistinct. The populations from the latter areas are almost indistinguishable from *bitaeniatus* on the basis of this character. This change is a rather gradual one and can be validly interpreted as what Brown and Wilson, 1956, have called "character displacement." This throat grooving is, I believe, a species-recognition character and one that has been acquired by *ellioti* in the eastern part of its range to enable the chameleons themselves to distinguish their

own species from the similarly proportioned and closely related *bitaeniatus* where these two taxa occur together. In areas a long distance from the zone of contact, there would be no selection for this character, and consequently one would expect it to be less well marked.

The evidence for *bitaeniatus* and *ellioti* demonstrates that they are most different where they are closest together and thus are, in all probability, species. However, this character displacement involves only *ellioti* and I have been unable to recognize any tendency to character modification in *bitaeniatus*.

The two forms may replace each other geographically because they are too similar ecologically to coexist. Evidence on this point is almost nonexistent, however, and we can say only that both seem to be animals associated with cultivation and savanna conditions rather than mountain rain forest, and even this is based on very little evidence as far as *bitaeniatus* is concerned.

C. ellioti is the only member of this group occurring in most of the lowlands of Uganda, but in the mountains that edge the west side of the Rift Valley it is replaced by yet another series of populations.

These mountain forms, the *rudis* group, are closely associated with the mountain forest and consist of a series of more or less isolated populations from the Ruwenzori on the north, south to the mountains east of Lake Nyasa with outliers on Mt. Kilimanjaro, Mt. Meru, at Embagi in northern Tanganyika, and single specimens assigned to this species are known from the Mau Escarpment in Kenya and from Gilo in the Sudan. All these agree in being squat chameleons with short, broad, heads and heterogeneous scalation.

In three of these areas, Mt. Ruwenzori, the mountains north of Kivu, and the mountains west of Lake Tanganyika, *ellioti* comes into contact with *rudis*. There is little evidence of the exact situation on Ruwenzori. In the mountains north of Lake Kivu, Witte records both forms from a large number of his collecting stations, with *ellioti* absent from the highest ones and *rudis* absent from the lowest ones, but with a broad zone of overlap. Laurent's account of the situation in these mountains shows similar distributional relationships, but he also notes that there is a marked ecological difference between the two, *ellioti* being an animal of the open, dryer areas, and *rudis* associated with the mountain forest. He notes that *ellioti* reaches high altitudes where the forest has been cut for cultivation. This situation probably is duplicated in the other mountain areas as well.

The extensive interdigitation of ranges, if not actual overlap, seems to me to make maintenance of two non-reproductively isolated lizard populations without any indication of intergradation highly improbable. The situation appears to parallel that of *bitaeniatus* and *höhnelii*, and I believe *ellioti* must be considered specifically distinct from the mountain forms.

It is interesting to note that the *ellioti* populations that occur in close proximity to the short-headed mountain forms have a head that is noticeably narrower than those *ellioti* which are sympatric with long-headed *bitaeniatus*. I believe that in chameleons, head and body shape can be a very important species recognition character and that this cline can be interpreted as another case of character displacement, on the same grounds that the geographical variation in throat grooves was so interpreted. This adds further weight to the opinion that *ellioti* is specifically distinct from *rudis*. These two clines, one in head shape, the other in throat grooving, are roughly parallel in that direction, but they do not run concordantly. In head shape, the area of most rapid change is in central Uganda between the Kenya populations and those of the Ruwenzori Mountains and southwestern Uganda. In throat grooving, the area of most rapid change is in southwestern Uganda between the populations of the Ruwenzori Mountains and north central Uganda and the populations of the area north of Lake Kivu.

C. rudis has been collected in numbers in four areas: the Ruwenzori Mountains; the mountains north of Lake Kivu; Mt. Kabobo; and Mt. Kilimanjaro and Mt. Meru. The population in each of these areas shows some peculiarity. In the Ruwenzori Mountains (*C. r. rudis*), some individuals have very long gular crests; in the Kivu area (also referred to *C. r. rudis*), some individuals have a small rostral protuberance; in the Mt. Kabobo area (*C. r. schoutedeni*), most individuals have the gular crest very reduced and the junction of the canthal ridges narrowly separated from the labials; on Mt. Kilimanjaro and Mt. Meru (*C. r. sternfeldi*), most individuals have the posterior end of the parietal crest much swollen.

I have also seen small samples, 1 to 3 specimens, from several other localities: Gilo, southern Anglo-Egyptian Sudan; Embagi, northern Tanganyika; and the Loita Plains, Mau Escarpment, Kenya. Hellmich (1956) describes two specimens from Litembo, Tanganyika, west of Lake Nyasa. None of these specimens match clearly the populations from the four areas mentioned above. This is primarily because they lack the peculiarities that

characterize these populations. Additional specimens might tie them to one or another of the better known populations but it seems equally probable that additional specimens would disclose characters that would distinguish them.

The pattern of geographical distribution and variation in *rudis* contrasts with that in *ellioti*. In *ellioti* the range is continuous, or nearly so, over most of the area where it occurs, and the geographical variation observed is more or less clinal in nature. In *rudis*, which is restricted to mountain forest, the distribution is apparently widely disjunct, and almost every one of the isolated populations shows some morphological peculiarity that distinguishes it from the rest of the species.

The remaining well defined species, *schubotzi*, is rather peculiar in several respects. It is known only from the top of Mt. Kenya, where it apparently lives in the alpine meadows above the range of *C. höhnelii*. It is a small chunky species, with a broad head and extremely heterogeneous lateral scalation, with the much enlarged plates strongly convex. It appears to be most closely related to *rudis*, but well-differentiated from it.

There is a single small specimen known from Mt. Kineti in the Imatong Mountains of the Anglo-Egyptian Sudan which Schmidt (1943) described as *C. kinetensis*. This specimen is most like *C. bitaeniatus* but has less heterogeneous scales and is, in this character, like *ellioti* which is known from the Imatong Mountains. With no more evidence than this single specimen, Schmidt's name cannot be assigned definitely to any known species and consequently is conserved.

All of these chameleons form a closely related complex. On the basis of the proportion and scale characters used here it is possible to distinguish several species. However, on these characters I cannot propose any definitive system of relationships among the species. I suspect that *ellioti* and *bitaeniatus* are closely related and that *höhnelii* is also related to *bitaeniatus*, while *rudis* and *schubotzi* are closely related to each other and a little more distantly to the other three. *C. kinetensis* seems also close to *bitaeniatus* and *ellioti*. This arrangement is based more on shape and proportions than scale characters and is only one of several groupings that could be proposed. Interspecific relationships in the genus *Chamaeleo* as a whole are poorly understood at present and it may well be necessary to consider characters in addition to the currently used externals before they are well understood.

Until the relationships are understood, any discussion of the

origin of the species must be tentative at best. I can only speculate that the barriers which in the past isolated populations of the ancestral "*bitaeniatus*" were ecological rather than physical in nature. Even today the various species seem to be restricted to certain types of habitat. The differentiation in the population of *C. rudis* on different mountains demonstrates the reduced gene flow between populations separated by unfavorable habitat and suggests one possible means of speciation. These populations of *rudis* seem most easily interpreted as relics of a period when the rainfall was higher and the forest which is now restricted to the mountains was much more extensive. This period of more widespread forest may equate with the last pluvial period in the Pleistocene of East Africa as has been suggested by Moreau, 1952. The decreasing rainfall which followed the pluvial maxima must have resulted in a retreat of the forests from the lower elevations to their present positions on the higher mountains. This fragmentation of the forests must also have meant a fragmentation of the population of chameleons living in them. Such a break-up of *rudis* into isolated populations, each subject to slightly different conditions and consequently different selection pressures, would have produced the differentiation discussed in this paper.

The origin of the several species undoubtedly lies further in the past than does the origin of the races of *rudis*. It seems quite possible that this speciation was also associated with the ecological changes of a complex sort which must have been associated with the Pleistocene climatic changes in East Africa.

SUMMARY

The chameleons of the *bitaeniatus* group are a closely related complex of forms in East Africa. Though most of the forms were originally described as species, they have in recent years been considered races of a single species. A re-examination of the material shows that apparently at least five and possibly six species are involved. One species was known from the very high altitudes of Mt. Kenya (*C. schubotzi*), two species from the lower elevations in the highlands (*C. bitaeniatus* in Kenya, Somali Republic, Ethiopia and extreme northern Tanganyika, and *C. ellioti* in Ruanda, Uganda, Anglo-Egyptian Sudan and extreme western Kenya), another (*C. rudis*) above *C. ellioti* in the mountains west of Lake Victoria and on Mt. Kilimanjaro and Mt. Meru. Each of these forms has a different geographical

range and in most places only a single taxon occurs. However, sympatry has been demonstrated between *höhnelii* and *bitaeniatus* and between *rudis* and *ellioti*. *C. bitaeniatus* and *ellioti* are not demonstrated to be sympatric but they show character displacement, becoming more different, where their ranges approach one another.

Two of these species show marked geographical variation. *C. ellioti* shows climatic variation apparently associated with character displacement. *C. rudis* occurs on separated mountains in isolated forest populations, three of which are recognized as different subspecies.

A single specimen from Anglo-Egyptian Sudan does not fit any of the other species and the name, *C. kinetensis*, proposed for it by Schmidt (1943) is retained.

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